

bee

Bees are any of 20,000 species of insects belonging to the superfamily Apoidea and the order Hymenoptera, including such important pollinators of plants as the bumblebees; the yellow-faced, or plasterer, bees; the mining, or burrower, bees; and the economically important honeybees of the genus *Apis*, the only domesticated insects besides the silkworm. Honeybees are known for the honey and wax they produce and their ability to communicate with one another through dancelike postures (the so-called dance language).

Only 500 species of bees are social; these include the bumblebees, the tropical stingless bees, and the honeybees. They form colonies of from several hundred to 80,000 individuals, organized in rigid caste systems, and secrete wax from which they build their nests.

Most other species of bees either are solitary—secreting no wax and nesting in the ground, hollow plant stems, or similar niches—or, like the cuckoo bees, are parasitic in the nests of others. The solitary bees, named for the material or method they use to construct nests for their young, include the plasterer, burrower, mining, mason, and leaf-cutter bees.

### BEES AND WASPS

Bees belong to the same order as wasps. Like wasps, bees have mouth parts adapted for both chewing and sucking, but the bee's tongue is longer than the wasp's and better suited for gathering nectar from a greater variety of flowers. As adults, bees and almost all wasps feed only on nectar or honey; young wasps are fed only insects and spiders, whereas young bees are fed only nectar and pollen. Nectar is a sugary substance produced at the base of petals in many flowers and made into honey by bees.

Some wasplike bees swallow pollen and nectar, which they regurgitate into the cells in which they lay their eggs. Most bees, however, are distinguished from wasps by modifications that enable them to collect pollen. Bees have branched and feathery (plumose) body hairs. Females have brushes on their legs, and they use these brushes to remove pollen that sticks to the body hairs. The pollen is then stored under the abdomen or on the broadened hind legs. The parasitic cuckoo bees, however, can be distinguished from wasps only by the presence of the branched hairs characteristic of bees.

### THE BEE FAMILIES

The Apoidea are subdivided into several families on the basis of how their wings are veined, and other criteria. Most of the 20,000 species are solitary bees. The queen constructs her own nest of one or more brood cells. She then stocks the cells with pollen and nectar to provide food for the larvae and deposits her eggs just before sealing the cell.

Some species are gregarious and place their nests in close proximity to each other. When such bees share a common entrance, a division of labor may be observed—for example, one bee may guard the entrance against parasites or predators. Bees are considered truly social when there is a single queen, when a worker caste of nonreproductive females shares in the construction of the nest and other duties, and when the larvae are fed gradually.

#### Halictidae and Andrenidae

The family Halictidae constitutes 60 to 70 percent of the Apoidea, and the family Andrenidae another 20 percent. Queens of these families dig simple or branched tunnels in the ground and construct cells of firmly tamped earth, lined with waterproof secretions from the salivary glands to maintain the humidity required by the larvae. Those that do not secrete such linings have larvae that spin cocoons. A mass of pollen mixed with nectar is placed in the cell; the shape of this mass varies among species. In all species, however, minimal contact occurs between the mass and the cell wall and serves to deter the growth of mold. One species makes its pollen ball with a tripod of three short legs.

An egg is laid in each cell, and the tunnel is filled with loose dirt. The hatched larva uses the pollen as food, then pupates and transforms into an adult—a complete metamorphosis—and finally digs itself out of the tunnel.

In four species of Halictidae, the brood cells are not capped but are left open for removal of larval skins, dead larvae, and feces. This represents another step in the evolution toward more complex social behavior for which a

mathematical genetic model has been formulated.

Halictidae are especially important because they include both the solitary and the truly social. The females that are produced in the fall eat only nectar before hibernating; but when they emerge in the spring they eat pollen, which stimulates ovarian development, and they undertake nesting.

One halactid, the alkali bee, *Nomia melandri*, nests in communities of thousands of individuals with almost 2,700 nests per square meter (250 per square foot). Eighty of these bees are equal to a small colony of honeybees in pollinating alfalfa blooms, and so farmers often establish alkali bees near alfalfa fields. A hectare of such nests is equal to almost 125 colonies of honeybees (1 acre = 50 colonies). The males of some species, on the other hand, stake out a territory and chase away all bees except females of their own species.

#### Megachilidae

The family Megachilidae includes the shiny, bluish-green mason bees (*Osmia*), which construct small cells in clusters of 10 to 30 under stones, in decaying wood, in empty snail shells, or in the deserted burrows of other bees. The leaf-cutting bees (*Megachile*) make cells by finding a niche in wood, under loose bark, or in the ground and lining it with neatly cut leaves. Oblong pieces of leaves are used for the sides, and circular pieces for the ends.

#### Xylocopidae

The large carpenter bees of the family Xylocopidae look like dark, shiny bumblebees without hair on the abdomen. They alarm anxious homeowners, sometimes with good reason, with their habit of digging burrows in wood porches and in barns. The excavations may be 1 m (3 ft) long and are often reused in successive years.

#### Bombidae

Bumblebees (Bombidae) leave their nest in the autumn, and the fertilized queens hibernate in some protected place during the winter. In the spring each queen builds a nest of moss or grass, preferably in a deserted rodent nest. From scales secreted by abdominal glands, she makes a honeypot of wax and then makes a cell and half fills it with pollen before depositing her eggs in it. The queen covers the eggs with a layer of wax and sits on them like a brooding hen, sipping honey from her pot. After the larvae hatch, they eat the pollen and grow, then spin cocoons in which to pupate. When the workers emerge, they cut away the upper half of the cells, and the remainder is used as a receptacle for nectar.

Bumblebee populations vary from year to year, depending on environmental factors; but one typical nest collected in Wisconsin contained one queen, 515 adult workers, 117 worker and 119 queen pupae, 101 larvae, 308 eggs contained in 18 cells on cylinders of pollen, and 709 empty worker cells filled with honey.

The larger workers maintain the covering over the nest and collect food, and the smaller ones care for the young larvae and do the inside work.

Only males are produced late in the summer, and female larvae literally may be jettisoned to control the population. When workers lay eggs, the queen may chase the workers away and eat the eggs; but if the queen dies or is removed, one of the larger workers will take her place within four hours or less. The difference in size of workers is dependent upon the amount of food they have available to eat when they are larvae.

Bumblebees are superior to other bees in pollinating red clover, since they have a tongue that is 2.5 mm (0.1 in) longer than that of honeybees. Artificial methods of rearing bumblebees have been successful, but a better technique may be to encourage natural populations by providing forage plants that bloom eight to nine weeks prior to red clover, so that the colonies have abundant food on which to rear brood.

#### Meliponidae

The stingless bees (Meliponidae) have acquired many methods of defense to replace their long-lost stinging apparatus. Several hundred species exist in the tropics and subtropics, with colonies ranging in size from a few hundred to 80,000 individuals.

The colonies nest in cavities and build walls, cells, and honeycombs of cerumen, which is a mixture of resin, wax, and sometimes mud. If the nest is in the open, the walls are as much as 20 cm (8 in) thick, with many separate layers

for insulation and protection. The small entrance hole may be guarded by a single bee. As among solitary bees, the brood cell is sealed after the egg is laid on stored food. Observers report that the queen eats both the food stored in brood cells and the unfertilized eggs, laid by workers, that would develop into males.

To establish a new nest, the workers select a site and seal all cracks with material brought from the parent colony. Honey and pollen are transferred, and males follow the workers to the new nest. When all is ready, a virgin queen flies from the old nest to the new one and soon makes a mating flight.

Before the introduction of honeybees from Europe, the only honey and wax available in South and Central America was that produced by stingless bees. The wax was used for casting gold ornaments, and the honey for alcoholic beverages used on ceremonial occasions. These bees are still being cultivated in various parts of the world.

#### Apidae

The family Apidae, which includes honeybees, no longer uses honeypots that could be damaged by exposure to the elements. Instead, honey and pollen are stored, and brood is reared, in vertical combs with a layer of cells on each face. Of the four species of honeybees in this family, three occur only in Asia: *Apis dorsata*, the giant Indian bee, which builds a single comb as large as 1.5 m (5 ft) wide and 1 m (3 ft) long attached to rocks, trees, or buildings; *A. florea*, with a single comb about 8 to 12 cm (3 to 5 in) across; and *A. indica*, the Oriental hive bee, with nests of several combs sheltered in crevices of rocks or hollows of trees.

*A. mellifera*, the western honeybee or hivebee, also builds its nest of many combs in sheltered places and is found in the United States, Europe, Anatolia, and Africa. Colonies kept in hives yield an average of 23 kg (50 pounds) of honey.

Numerous geographic races have arisen as a result of natural selection. The brown or black German bees were imported from Europe to America by the early colonists. The Italian race was imported to Long Island in 1860; it is now the most common commercial variety, with Caucasians the second most popular. The so-called killer bees, of African origin and accidentally released in South America in the mid-1950s, are more aggressive and likely to sting intruders. They are also more inclined to swarm and are unsuitable for commercial beekeeping. (See BEE, KILLER.)

Unlike other bees, honeybees do not hibernate during cold weather. They last out the rigors of northern winters by feeding on stored supplies and sharing their body heat, clustering together in dense packs.

Socialization is most advanced in the Apidae. As new, young queens are about to emerge in an established hive, half of the colony leaves with the old queen and clusters on a nearby bush or tree while scout bees search for a new home. When the scouts appear to agree on a new location, the swarm departs. At the old nest, meanwhile, the first queen to emerge disposes of the other queens (by stinging them) before they have a chance to emerge. Within a few days, the virgin queen will fly to where drones assemble, and mate with 6 to 12 drones. The sperm from these drones is stored in a sac (spermatheca) and used during her egg-laying life of from two to five years or a maximum of nine.

Honeybees are subject to various diseases and parasites, including the bee mite, *Acarapis woodi*, which weakens bees and reduces their honeymaking and pollinating abilities. Legislation enacted in the United States in 1922 to regulate importation of honeybees was thought to have prevented this infestation, which has caused serious losses in other countries, but in 1984 the mite was found in New York, Florida, Texas, Louisiana, and South Dakota. As a result, more than 150 million honeybees were destroyed by beekeepers to prevent further spread of the mite.

#### DRONES AND WORKERS

Drones develop by parthenogenesis from unfertilized eggs that the queen produces by withholding sperm from the eggs laid in large drone cells. Drones lack stings and the structures needed for pollen collection; in the autumn they are ejected by the colony to starve, unless the colony is queenless. New drones are produced in the spring for mating.

Both queens and workers are produced from fertilized eggs. Queen larvae are reared in special peanut-shaped cells and fed more of the pharyngeal gland secretions of the nurse bees (bee milk or royal jelly) than the worker larvae are. The precise mechanism for this caste differentiation is still uncertain. Although workers are similar in appearance and behavior to other female bees, they lack the structures for mating. When no queen is present to

inhibit the development of their ovaries, however, workers eventually begin to lay eggs that develop into drones.

## PHEROMONES

The integrity of the colony is maintained by chemical secretions, or PHEROMONES. Workers secrete pheromones from the so-called Nasanov gland at the tip of the abdomen when they cluster, enter a new nesting site, or mark a source of nectar or water. The colony scent is recognizable by bees of the same colony because of its unique combination of components derived from the colony's particular collections of nectar and pollen.

When queens fly to mate, a mandibular-gland pheromone attracts the drones. The same gland produces another pheromone, called queen substance, which workers lick from the queen's body and pass along as they exchange food with one another. The eaten pheromone inhibits the ovaries of workers; when the queen's secretion is inadequate, the colony produces queen cells to supersede her.

The mandibular glands of workers produce an alarm odor, which serves to alert the colony when it is disturbed. Workers also produce a sting odor, which is released at the site of the sting and serves to direct other bees to the sting area. Stingless bees bite leaves at intervals along their flight path to provide a scent trail of mandibular secretions.

## DANCE LANGUAGE

The ability of honeybees to communicate direction and distance from the hive to nectar sources through dance "language" has received widespread attention. In 1973, Karl von FRISCH received a Nobel Prize for deciphering the language, which consists of two basic dances: a dance in a circle, for indicating sources without reference to specific distance or direction; and a tail-wagging dance in which the exact distance is indicated by a number of straight runs with abdominal wagging—the fewer runs per minute, the farther away the source. Wing vibrations produce sounds at the same rate as the tail wagging and are detected by organs in the legs of other bees. Researchers have developed a robot "bee" that can communicate with other bees in this way (see ANIMAL COMMUNICATION).

The various species of *Apis*, and races of *A. mellifera*, indicate a particular distance by a different dance tempo. This may lead the individuals in colonies with a mixture of races to misunderstand messages about the distance to a feeding site. Stingless bees communicate only by sounds.

The direction, or azimuth, to the food source is indicated by the angle of the wagging dance to the Sun. That is, bees use the Sun as a compass, orienting the dance angle to the plane of polarization of the sunlight. Even when the Sun is obscured by clouds, bees can detect its position from the light in brighter patches of the sky. Ultraviolet designs in flowers serve as nectar guides to blooms in areas as small as 4 sq m (43 sq ft<sup>2</sup>).

Honeybees also have a little-understood, built-in clock that appears to be synchronized with the store of nectar in flowers. Hence, honeybees making the rounds of flowers in search of nectar always seem to be at the right place at the right time.

Toge S. K. Johansson

Bibliography: Goodman, L. J., and Fisher, R. C., eds., *The Behaviour and Physiology of Bees* (1991); Gould, J. L. and C. G., *The Honey Bee* (1988); Hubbell, S., *A Book of Bees* (1988); Michener, C. D., et al., *The Bee Genera of North and Central America* (1994); O'Toole, C., and Raw, A., *Bees of the World* (1992); Seeley, T. D., *Honeybee Ecology* (1985); Winston, M., *The Biology of the Honeybee* (1987); and *Killer Bees* (1992).

## beekeeping

Beekeeping, or apiculture, is the cultivation of colonies of honeybees. Commercial beekeeping includes the production of HONEY and beeswax, the breeding of bees for sale, and the rental of bees for pollinating crops. Beekeeping in most of the world means cultivating the western honeybee, *Apis mellifera* (see BEE). The aggressive killer bee, a relative of the African honeybee, *A. mellifera scutellata*, however, is unsuitable for commercial beekeeping (see BEE, KILLER). In parts of Asia the eastern honeybee, *A. indica*, is cultivated, as is, on an experimental basis, the giant honeybee, *A. dorsata*.

Modern beekeeping is based on the ancient Greek technique of creating a so-called bee space. The hive comprised a basket containing a series of parallel wooden bars separated by a distance equal to that between honeycombs naturally built by bees. That distance is 6.350-9.525 mm (0.25-0.375 in), and any departure from this range results in the space being filled with comb or propolis. A honeycomb is a mass of hexagonal cells in the nest that contain brood and honey.

A beehive based on the ancient principle was developed (1851) in the United States by Lorenzo Lorraine Langstroth. The typical beehive today comprises a bottom board and several boxes containing movable frames and a cover. Each frame is furnished with a beeswax foundation imprinted with the hexagonal shapes of cell bottoms. The bees are guided by the imprinted cells in building their honeycombs.

## THE POLLINATOR INDUSTRY

The world's annual production of more than 1,000,000 metric tons (1,102,000 U.S. tons) of honey could be replaced with other sugar products, but the services of honeybees as pollinators of some 90 crops would be lost. Mixed farming as practiced on small family farms has given way to more efficient single-crop agribusiness, leaving little or no wasteland where bees can find nesting sites or weeds that supply nectar and pollen. The use of pesticides to control harmful insects has also reduced the population of beneficial insects such as pollinators. Thus, fruit and seed growers contract with beekeepers to move honeybee colonies onto the farms. This ensures income to the beekeeper during years when honey production fails. The moving, however, increases the risk of spreading American foulbrood, a virulent disease of bees, so some beekeepers routinely feed antibiotics to avoid losses.

In North America new colonies are established with packages of bees, each container weighing 0.9 to 2.26 kg (2 to 5 lb), or small colonies called nuclei, shipped from breeders in the southern states. It is unlikely that a crop can be harvested from these colonies in the first season, because a hive requires 40.82 kg (90 lb) of honey for overwintering.

Toge S. K. Johansson

Bibliography: Goodman, L. J., and Fisher, R. C., eds., *The Behavior and Physiology of Bees* (1991); Graham, J. M., ed., *The Hive and the Honey Bee* (1992); Hubbell, S., *A Book of Bees* (1989); Morse, R., and Flottum, K., eds., *The ABC and XYZ of Bee Culture* (1990); Whynott, D., *Following the Bloom* (1992).

## bee

Bees are any of 20,000 species of insects belonging to the superfamily Apoidea and the order Hymenoptera, including such important pollinators of plants as the bumblebees; the yellow-faced, or plasterer, bees; the mining, or burrower, bees; and the economically important honeybees of the genus *Apis*, the only domesticated insects besides the silkworm. Honeybees are known for the honey and wax they produce and their ability to communicate with one another through dancelike postures (the so-called dance language).

Only 500 species of bees are social; these include the bumblebees, the tropical stingless bees, and the honeybees. They form colonies of from several hundred to 80,000 individuals, organized in rigid caste systems, and secrete wax from which they build their nests.

Most other species of bees either are solitary—secreting no wax and nesting in the ground, hollow plant stems, or similar niches—or, like the cuckoo bees, are parasitic in the nests of others. The solitary bees, named for the material or method they use to construct nests for their young, include the plasterer, burrower, mining, mason, and leaf-cutter bees.

## BEES AND WASPS

Bees belong to the same order as wasps. Like wasps, bees have mouth parts adapted for both chewing and sucking, but the bee's tongue is longer than the wasp's and better suited for gathering nectar from a greater variety of flowers. As adults, bees and almost all wasps feed only on nectar or honey; young wasps are fed only insects and spiders, whereas young bees are fed only nectar and pollen. Nectar is a sugary substance produced at the base of petals in many flowers and made into honey by bees.

Some wasplike bees swallow pollen and nectar, which they regurgitate into the cells in which they lay their eggs. Most bees, however, are distinguished from wasps by modifications that enable them to collect pollen. Bees have branched and feathery (plumose) body hairs. Females have brushes on their legs, and they use these brushes to remove pollen that sticks to the body hairs. The pollen is then stored under the abdomen or on the broadened hind legs. The parasitic cuckoo bees, however, can be distinguished from wasps only by the presence of the branched hairs characteristic of bees.

## THE BEE FAMILIES

The Apoidea are subdivided into several families on the basis of how their wings are veined, and other criteria. Most of the 20,000 species are solitary bees. The queen constructs her own nest of one or more brood cells. She then stocks the cells with pollen and nectar to provide food for the larvae and deposits her eggs just before sealing the cell.

Some species are gregarious and place their nests in close proximity to each other. When such bees share a common entrance, a division of labor may be observed—for example, one bee may guard the entrance against parasites or predators. Bees are considered truly social when there is a single queen, when a worker caste of nonreproductive females shares in the construction of the nest and other duties, and when the larvae are fed gradually.

### Halictidae and Andrenidae

The family Halictidae constitutes 60 to 70 percent of the Apoidea, and the family Andrenidae another 20 percent. Queens of these families dig simple or branched tunnels in the ground and construct cells of firmly tamped earth, lined with waterproof secretions from the salivary glands to maintain the humidity required by the larvae. Those that do not secrete such linings have larvae that spin cocoons. A mass of pollen mixed with nectar is placed in the cell; the shape of this mass varies among species. In all species, however, minimal contact occurs between the mass and the cell wall and serves to deter the growth of mold. One species makes its pollen ball with a tripod of three short legs.

An egg is laid in each cell, and the tunnel is filled with loose dirt. The hatched larva uses the pollen as food, then pupates and transforms into an adult—a complete metamorphosis—and finally digs itself out of the tunnel.

In four species of Halictidae, the brood cells are not capped but are left open for removal of larval skins, dead larvae, and feces. This represents another step in the evolution toward more complex social behavior for which a

mathematical genetic model has been formulated.

Halictidae are especially important because they include both the solitary and the truly social. The females that are produced in the fall eat only nectar before hibernating; but when they emerge in the spring they eat pollen, which stimulates ovarian development, and they undertake nesting.

One halactid, the alkali bee, *Nomia melandri*, nests in communities of thousands of individuals with almost 2,700 nests per square meter (250 per square foot). Eighty of these bees are equal to a small colony of honeybees in pollinating alfalfa blooms, and so farmers often establish alkali bees near alfalfa fields. A hectare of such nests is equal to almost 125 colonies of honeybees (1 acre = 50 colonies). The males of some species, on the other hand, stake out a territory and chase away all bees except females of their own species.

#### Megachilidae

The family Megachilidae includes the shiny, bluish-green mason bees (*Osmia*), which construct small cells in clusters of 10 to 30 under stones, in decaying wood, in empty snail shells, or in the deserted burrows of other bees. The leaf-cutting bees (*Megachile*) make cells by finding a niche in wood, under loose bark, or in the ground and lining it with neatly cut leaves. Oblong pieces of leaves are used for the sides, and circular pieces for the ends.

#### Xylocopidae

The large carpenter bees of the family Xylocopidae look like dark, shiny bumblebees without hair on the abdomen. They alarm anxious homeowners, sometimes with good reason, with their habit of digging burrows in wood porches and in barns. The excavations may be 1 m (3 ft) long and are often reused in successive years.

#### Bombidae

Bumblebees (Bombidae) leave their nest in the autumn, and the fertilized queens hibernate in some protected place during the winter. In the spring each queen builds a nest of moss or grass, preferably in a deserted rodent nest. From scales secreted by abdominal glands, she makes a honeypot of wax and then makes a cell and half fills it with pollen before depositing her eggs in it. The queen covers the eggs with a layer of wax and sits on them like a brooding hen, sipping honey from her pot. After the larvae hatch, they eat the pollen and grow, then spin cocoons in which to pupate. When the workers emerge, they cut away the upper half of the cells, and the remainder is used as a receptacle for nectar.

Bumblebee populations vary from year to year, depending on environmental factors; but one typical nest collected in Wisconsin contained one queen, 515 adult workers, 117 worker and 119 queen pupae, 101 larvae, 308 eggs contained in 18 cells on cylinders of pollen, and 709 empty worker cells filled with honey.

The larger workers maintain the covering over the nest and collect food, and the smaller ones care for the young larvae and do the inside work.

Only males are produced late in the summer, and female larvae literally may be jettisoned to control the population. When workers lay eggs, the queen may chase the workers away and eat the eggs; but if the queen dies or is removed, one of the larger workers will take her place within four hours or less. The difference in size of workers is dependent upon the amount of food they have available to eat when they are larvae.

Bumblebees are superior to other bees in pollinating red clover, since they have a tongue that is 2.5 mm (0.1 in) longer than that of honeybees. Artificial methods of rearing bumblebees have been successful, but a better technique may be to encourage natural populations by providing forage plants that bloom eight to nine weeks prior to red clover, so that the colonies have abundant food on which to rear brood.

#### Meliponidae

The stingless bees (Meliponidae) have acquired many methods of defense to replace their long-lost stinging apparatus. Several hundred species exist in the tropics and subtropics, with colonies ranging in size from a few hundred to 80,000 individuals.

The colonies nest in cavities and build walls, cells, and honeypots of cerumen, which is a mixture of resin, wax, and sometimes mud. If the nest is in the open, the walls are as much as 20 cm (8 in) thick, with many separate layers

for insulation and protection. The small entrance hole may be guarded by a single bee. As among solitary bees, the brood cell is sealed after the egg is laid on stored food. Observers report that the queen eats both the food stored in brood cells and the unfertilized eggs, laid by workers, that would develop into males.

To establish a new nest, the workers select a site and seal all cracks with material brought from the parent colony. Honey and pollen are transferred, and males follow the workers to the new nest. When all is ready, a virgin queen flies from the old nest to the new one and soon makes a mating flight.

Before the introduction of honeybees from Europe, the only honey and wax available in South and Central America was that produced by stingless bees. The wax was used for casting gold ornaments, and the honey for alcoholic beverages used on ceremonial occasions. These bees are still being cultivated in various parts of the world.

#### Apidae

The family Apidae, which includes honeybees, no longer uses honeypots that could be damaged by exposure to the elements. Instead, honey and pollen are stored, and brood is reared, in vertical combs with a layer of cells on each face. Of the four species of honeybees in this family, three occur only in Asia: *Apis dorsata*, the giant Indian bee, which builds a single comb as large as 1.5 m (5 ft) wide and 1 m (3 ft) long attached to rocks, trees, or buildings; *A. florea*, with a single comb about 8 to 12 cm (3 to 5 in) across; and *A. indica*, the Oriental hive bee, with nests of several combs sheltered in crevices of rocks or hollows of trees.

*A. mellifera*, the western honeybee or hivebee, also builds its nest of many combs in sheltered places and is found in the United States, Europe, Anatolia, and Africa. Colonies kept in hives yield an average of 23 kg (50 pounds) of honey.

Numerous geographic races have arisen as a result of natural selection. The brown or black German bees were imported from Europe to America by the early colonists. The Italian race was imported to Long Island in 1860; it is now the most common commercial variety, with Caucasians the second most popular. The so-called killer bees, of African origin and accidentally released in South America in the mid-1950s, are more aggressive and likely to sting intruders. They are also more inclined to swarm and are unsuitable for commercial beekeeping. (See BEE, KILLER.)

Unlike other bees, honeybees do not hibernate during cold weather. They last out the rigors of northern winters by feeding on stored supplies and sharing their body heat, clustering together in dense packs.

Socialization is most advanced in the Apidae. As new, young queens are about to emerge in an established hive, half of the colony leaves with the old queen and clusters on a nearby bush or tree while scout bees search for a new home. When the scouts appear to agree on a new location, the swarm departs. At the old nest, meanwhile, the first queen to emerge disposes of the other queens (by stinging them) before they have a chance to emerge. Within a few days, the virgin queen will fly to where drones assemble, and mate with 6 to 12 drones. The sperm from these drones is stored in a sac (spermatheca) and used during her egg-laying life of from two to five years or a maximum of nine.

Honeybees are subject to various diseases and parasites, including the bee mite, *Acarapis woodi*, which weakens bees and reduces their honeymaking and pollinating abilities. Legislation enacted in the United States in 1922 to regulate importation of honeybees was thought to have prevented this infestation, which has caused serious losses in other countries, but in 1984 the mite was found in New York, Florida, Texas, Louisiana, and South Dakota. As a result, more than 150 million honeybees were destroyed by beekeepers to prevent further spread of the mite.

#### DRONES AND WORKERS

Drones develop by parthenogenesis from unfertilized eggs that the queen produces by withholding sperm from the eggs laid in large drone cells. Drones lack stings and the structures needed for pollen collection; in the autumn they are ejected by the colony to starve, unless the colony is queenless. New drones are produced in the spring for mating.

Both queens and workers are produced from fertilized eggs. Queen larvae are reared in special peanut-shaped cells and fed more of the pharyngeal gland secretions of the nurse bees (bee milk or royal jelly) than the worker larvae are. The precise mechanism for this caste differentiation is still uncertain. Although workers are similar in appearance and behavior to other female bees, they lack the structures for mating. When no queen is present to

inhibit the development of their ovaries, however, workers eventually begin to lay eggs that develop into drones.

## PHEROMONES

The integrity of the colony is maintained by chemical secretions, or PHEROMONES. Workers secrete pheromones from the so-called Nasanov gland at the tip of the abdomen when they cluster, enter a new nesting site, or mark a source of nectar or water. The colony scent is recognizable by bees of the same colony because of its unique combination of components derived from the colony's particular collections of nectar and pollen.

When queens fly to mate, a mandibular-gland pheromone attracts the drones. The same gland produces another pheromone, called queen substance, which workers lick from the queen's body and pass along as they exchange food with one another. The eaten pheromone inhibits the ovaries of workers; when the queen's secretion is inadequate, the colony produces queen cells to supersede her.

The mandibular glands of workers produce an alarm odor, which serves to alert the colony when it is disturbed. Workers also produce a sting odor, which is released at the site of the sting and serves to direct other bees to the sting area. Stingless bees bite leaves at intervals along their flight path to provide a scent trail of mandibular secretions.

## DANCE LANGUAGE

The ability of honeybees to communicate direction and distance from the hive to nectar sources through dance "language" has received widespread attention. In 1973, Karl von FRISCH received a Nobel Prize for deciphering the language, which consists of two basic dances: a dance in a circle, for indicating sources without reference to specific distance or direction; and a tail-wagging dance in which the exact distance is indicated by a number of straight runs with abdominal wagging—the fewer runs per minute, the farther away the source. Wing vibrations produce sounds at the same rate as the tail wagging and are detected by organs in the legs of other bees. Researchers have developed a robot "bee" that can communicate with other bees in this way (see ANIMAL COMMUNICATION).

The various species of *Apis*, and races of *A. mellifera*, indicate a particular distance by a different dance tempo. This may lead the individuals in colonies with a mixture of races to misunderstand messages about the distance to a feeding site. Stingless bees communicate only by sounds.

The direction, or azimuth, to the food source is indicated by the angle of the wagging dance to the Sun. That is, bees use the Sun as a compass, orienting the dance angle to the plane of polarization of the sunlight. Even when the Sun is obscured by clouds, bees can detect its position from the light in brighter patches of the sky. Ultraviolet designs in flowers serve as nectar guides to blooms in areas as small as 4 sq m (43 sq ft<sup>2</sup>).

Honeybees also have a little-understood, built-in clock that appears to be synchronized with the store of nectar in flowers. Hence, honeybees making the rounds of flowers in search of nectar always seem to be at the right place at the right time.

Toge S. K. Johansson

Bibliography: Goodman, L. J., and Fisher, R. C., eds., *The Behaviour and Physiology of Bees* (1991); Gould, J. L. and C. G., *The Honey Bee* (1988); Hubbell, S., *A Book of Bees* (1988); Michener, C. D., et al., *The Bee Genera of North and Central America* (1994); O'Toole, C., and Raw, A., *Bees of the World* (1992); Seeley, T. D., *Honeybee Ecology* (1985); Winston, M., *The Biology of the Honeybee* (1987); and *Killer Bees* (1992).